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Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change

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Abstract

1. Climate change impacts forest functioning and dynamics, and large uncertainties remain regarding the interactions between species composition, demographic processes and environmental drivers. There are few robust tools available to link these processes, which precludes accurate projections and recommendations for long-term forest management. Forest gap models present a balance between complexity and generality and are widely used in predictive forest ecology. However, their relevance to tackle questions about the links between species composition, climate and forest functioning is unclear. In this regard, demonstrating the ability of gap models to predict the growth of forest stands at the annual parameterization scale resolution—representing a sensitive and integrated signal of tree functioning and mortality risk—appears as a fundamental step.
2. In this study, we aimed at assessing the ability of a gap model to accurately predict forest growth in the short term and potential community composition in the long term, across a wide range of species and environmental conditions. To do so, we present the gap model ForCEEPS, calibrated using an original parameterization procedure for the main tree species in France.
3. ForCEEPS was shown to satisfactorily predict forest annual growth (averaged over a few years) at the plot level from mountain to Mediterranean climates, regardless of the species. Such an accuracy was not gained at the cost of losing precision for long-term predictions, as the model showed a strong ability to predict potential community compositions. The mechanistic relevance of ForCEEPS parameterization was explored by showing the congruence between the values of key model parameter and species functional traits.

4. We further showed that accounting for the spatial configuration of crowns within forest stands, the effects of climatic constraints and the variability of shade tolerances in the species community are all crucial to better predict short-term productivity with gap models.
5. *Synthesis*. The dual ability of predicting short-term functioning and long-term community composition, as well as the balance between generality and realism (i.e. predicting accuracy) of the new generation of gap models may open great perspectives for the exploration of the biodiversity–ecosystem functioning relationships, species coexistence mechanisms and the impacts of climate change on forest ecosystems.

KEYWORDS
climate, community composition, ecosystem functioning, forests, process-based modelling, productivity, traits

1 | INTRODUCTION

Forests cover about 30% of the land at the global scale, harbour most of terrestrial biodiversity, are an important carbon sink (Pan et al., 2011), play a pivotal role for climate regulation (Chapin et al., 2008) and provide key ecosystem services to humans (TEEB, 2010). However, climate change puts forests at high risk, including disruption in forest dynamics (McDowell et al., 2020), as harsher environmental conditions strongly impact forest structure and composition (Esquivel-Muelbert et al., 2019) and functioning (Allen et al., 2010; Boisvenue & Running, 2006; Lindner et al., 2010). In turn, compositional changes have been shown to affect forest functioning (Liang et al., 2016; Nadrowski et al., 2010), in interaction with climatic drivers (Coomes et al., 2014; Jactel et al., 2018). Yet, we lack robust tools to explore the interactive effects of biodiversity and climate change on forest dynamics and functioning.

Trees are long-lived organisms, which complicates the implementation of experiments designed to assess the influences of future environmental conditions (e.g. increased atmospheric CO_2 (Korner et al., 2005) or water stress (Limousin et al., 2009)) and community composition (Castagneyrol et al., 2013; Verheyen et al., 2016) on forest ecosystem functioning. While such experiments are key to study forest ecosystems, they require years to yield relevant results, and are necessarily conditioned by specific site conditions, thereby limiting their generality (Nadrowski et al., 2010; Norby & Zak, 2011). An alternative approach lies in the design of field sampling along climate and/or diversity gradients, which has shown significant results in the last years (e.g. Jourdan, Lebourgeois, et al., 2019; Jucker et al., 2016; del Río et al., 2017).

Complementing these approaches, forest models represent a crucial tool to explore the interactions and feedbacks among species composition, forest functioning and climate (Cordonnier, Kunstler, et al., 2018). Yet, the term 'forest models' covers a wide range of approaches, as recently reviewed (Pretzsch et al., 2015; Ruiz-Benito et al., 2020). Forest models were indeed used to predicting forest functioning and growth at scales ranging from tree, to stand (Makela et al., 2000) and landscape (Albrich et al., 2020; Pacala et al., 1993). Moreover, forest models differ in their complexity, from empirical yield tables (Skovsgaard & Vanclay, 2008) to ecophysiology-based models (Dufrêne et al., 2005; Simioni et al., 2016) that explicitly describe part of the biological mechanisms at stake but require a large amount of data to be properly calibrated and forced. Alternatively, forest gap models (hereafter referred to as 'gap models'), operating mostly at the stand scale, rely on empirical relationships, physiological knowledge and first principles from ecological theory (Bugmann, 2001). Because these models incorporate physically or ecologically-based hypotheses while relying on a small set of species-specific parameters, we believe that they are good candidates to explore forest responses to future growing conditions across spatial scales.

The design of gap model was originally motivated by the recognition that canopy gaps created by falling trees are a key driver shaping forest structure, dynamics and succession (Botkin et al., 1972). Although gap models also incorporate representations of abiotic constraints (e.g. water or nutrient stress) on forest functioning, and in some instances competition for below-ground resources, their key feature is a representation of the ability of trees of contrasted sizes and different species to compete for light resource. Gap models have been originally developed to understand the processes at play during forest succession (Botkin et al., 1972; Bugmann, 2001; Canham et al., 1994). Consequently, they are commonly validated against potential natural vegetation (hereafter 'PNV'), or against standing biomass accumulated over long (>50 years) time periods at the tree or stand level (Bugmann, 1996; Didion et al., 2009; Rasche et al., 2011; Strigul et al., 2008).

Recent developments have shown that gap models can be used to explore species coexistence mechanisms (Chauvet et al., 2017), diversity effects on the functioning of forest ecosystems (Bohn & Huth, 2017; Morin et al., 2011) and their response to climate change (Morin et al., 2018). These new perspectives highlight the importance

of forest structure and light-related interactions for forest functioning. In fact, forest structure has been shown to influence forest growth (Gough et al., 2019; Hardiman et al., 2011) and to partly mediate tree diversity effects on productivity (Cordonnier et al., 2019; Dănescu et al., 2016; Schnabel et al., 2019). Enhanced canopy space occupation ('canopy packing', Jucker et al., 2015) and light capture, which is mediated by the coexistence of species with contrasting shade tolerance, were shown to be crucial in the functioning of diverse and structurally complex forests (Williams et al., 2017). The presence of shade-tolerant species in tree species mixtures indeed strongly modulates the way tree diversity affects forest functioning and productivity (Cordonnier, Bourdier, et al., 2018; Toïgo et al., 2018; Van de Peer et al., 2018). Gap models can be parameterized for a wide range of species and environmental conditions, and could thus be a crucial tool to explore how differences in shade-tolerance affect the relationships between species richness and forest functioning (Morin et al., 2011; Toïgo et al., 2018). However, the multi-dimensional configuration of crowns in forest stands is not often represented explicitly in gap models (but see Maréchaux & Chave, 2017; Pacala et al., 1993; Purves et al., 2008), which hinders the assessment of the importance of architectural plasticity and canopy packing on forest productivity, species succession and coexistence.

Moreover, exploring Biodiversity–Ecosystem Functioning (BEF) relationships or species coexistence under climate change using gap models will require to assess (a) whether they are able to predict key patterns linking forest composition and functioning and (b) whether they embed a sound representation of the underlying mechanistic processes. Annual tree growth was shown to be a sensitive and integrated signal of tree functioning and mortality risk (Cailleret et al., 2017; DeSoto et al., 2020; Dobbertin, 2005; IFN, 2016), in contrast to PNV and standing biomass, which result from the accumulated effects of multiple ecological processes (e.g. tree recruitment, growth and mortality). Demonstrating the ability of gap models to predict the growth of forest stands at the annual time step or across a few years (i.e. to predict biomass *fluxes* in addition to biomass *stocks*; Guillemot et al., 2017) would open important research avenues to investigate how the mechanisms underlying BEF-relationships shape forest dynamics and community assembly (Cordonnier, Kunstler, et al., 2018). In addition, progress in trait-based ecophysiology has allowed identifying key functional traits involved in tree survival and growth in contrasting environments (Falster et al., 2018). Testing the congruence between key model parameters and functional traits is thus another way to evaluate the mechanistic relevance of these models.

Here, we aim to test whether a gap model can predict the annual growth of forests differing widely in species composition and climatic conditions throughout France, using only a small set of parameters that can be calibrated based on forest inventories. French mainland forests are found in a wide range of conditions including mountain, continental, oceanic and Mediterranean climates (Verkerk et al., 2019) and are therefore ideal to evaluate the generality of the hypotheses embedded in models. We present the ForCEEPS model (Forest Community Ecology and Ecosystem ProcesseS), derived from ForClim (Bugmann, 1996; Didion et al., 2009). Among other novelties, ForCEEPS embeds an improved representation of tree–tree competition for light by considering individual crown sizes in the vertical canopy space. ForCEEPS was parameterized for the main French tree species, and evaluated against annual growth (averaged across a few years) at the tree and stand scale, and against PNV. In addition, we verified the mechanistic relevance of ForCEEPS by assessing the congruence of key species parameters with functional traits. Finally, we conducted a sensitivity analysis on the ForCEEPS stand growth predictions, to quantify the importance of (a) an explicit representation of crown size, (b) the variability of shade tolerance among species and (c) the climatic constraints for accurately simulating stand growth.

2 | MODEL DESCRIPTION

2.1 | Overview

The ForCEEPS model is a forest gap model. Forest gap models simulate abiotic (climate and soil properties) and biotic constraints (tree–tree competition for light) on tree establishment, growth and survival in small parcels of land ('patches'). The mechanisms embedded in gap models rely on ecological hypotheses clearly stated, such as the trade-off between growth in full light and survival under shade (Bazzaz, 1979). Tree height and crown dimensions are inferred from allometry, based on tree trunk diameter, which is also the main variable measured in forestry surveys. Gap models commonly simulate forest dynamics at an annual time step, and do not explicitly represent biogeochemical cycling. ForCEEPS shares many features with the JABOWA (Botkin et al., 1972) and ForCLIM (Bugmann, 1996) models, and more precisely with ForCLIM 2.9.6 (Didion et al., 2009). Below, we present the central principles of ForCEEPS and the key developments that differentiate it from other gap models (a full description of the model is provided in Appendix A, but a simplified scheme is shown in Figure 1).

The simulated patches are independent from each other, with partly stochastic dynamics leading to differences among patches, and properties at the forest level are obtained by aggregating the properties over all patches (Bugmann, 2001; Shugart, 1984). Within each patch (i.e. usually between 400 and 1,000 m^2), environmental conditions are assumed to be horizontally homogeneous. The spatial location of trees is therefore implicit, and the competitive ability of a tree is assumed equal for all trees of similar size and species. This hypothesis allows for several simplifications in the representation of tree–tree interactions, but imposes that the patch size cannot be larger than *c*. 1,000 m^2, which is assumed to be the maximum area influenced by a single tree (Shugart, 1984). Gap models are often cohort-based, assuming that all trees of the same species and age behave similarly, for the sake of simulation efficiency. By contrast, ForCEEPS is completely individual-based, which notably allows to simulate the intraspecific variability in competitive ability. Another novel aspect in ForCEEPS is the possibility of imposing a feedback between the actual forest composition and

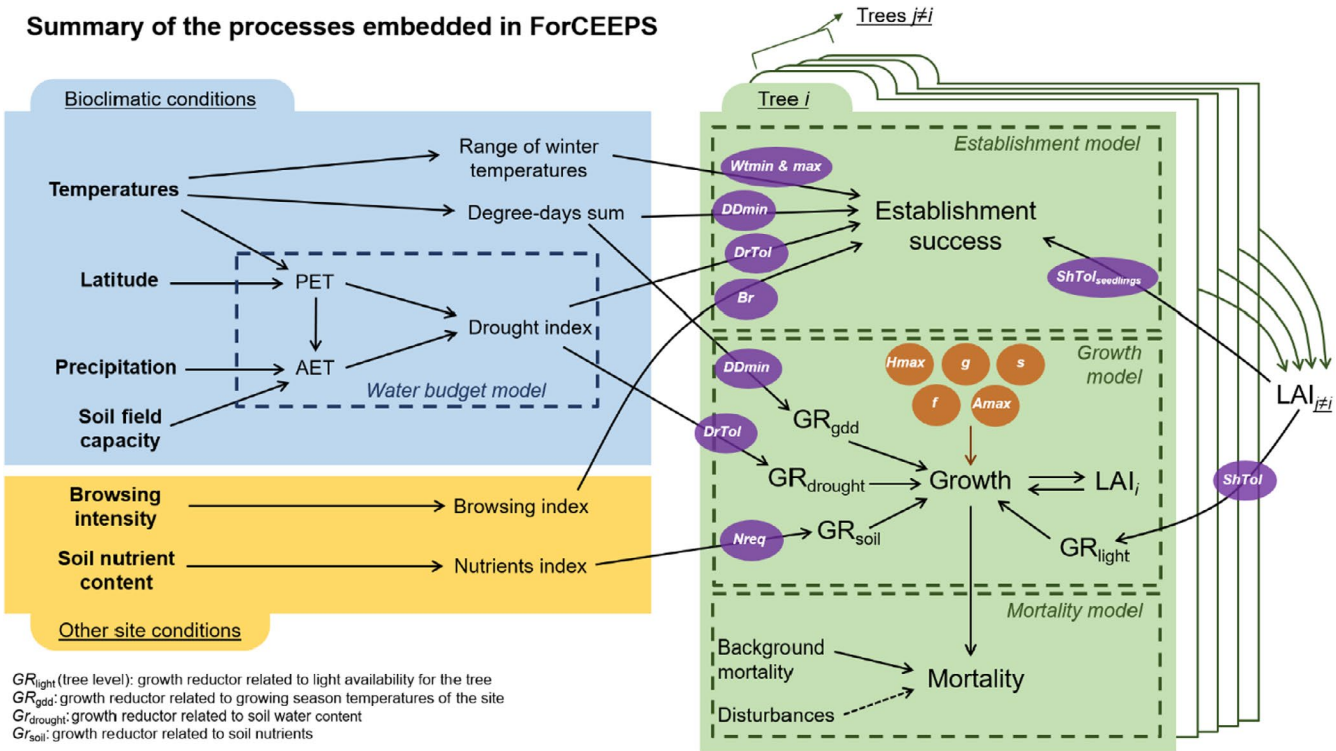

FIGURE 1 Detailed processes embedded in the ForCEEPS model. Species parameters (orange: intrinsic parameters; purple: response-to-drivers parameters) are described in Table 1. Further details are shown in Appendix A

the identity of the colonizing seedlings each year. This latter feature may be crucial for examining mechanisms of species coexistence in tree communities (Cordonnier, Kunstler, et al., 2018). However, with regard to the objective of the present paper, the most crucial development of ForCEEPS in comparison with ForClim is the implementation of a new module for tree–tree competition for light, that is, a key factor controlling growth and forest structure (Schwinning & Weiner, 1998), where the individual crown lengths are explicitly represented in the vertical canopy space (Appendix A).

Tree establishment, growth and mortality are simulated at a yearly time step, but monthly climatic data (monthly mean temperature and precipitation sum) are used to estimate annual or seasonal degree-days sum (GDD), winter temperatures and a drought index (DrI). The latter depends on monthly soil water content (SWC) that is calculated from a monthly water budget (Bugmann & Solomon, 2000) and is influenced by the site-specific maximum soil water holding capacity. Last, soil nutrients content (N_{soil}) is another abiotic factor simulated in ForCEEPS, considered constant at the site level (Appendix A).

2.2 | Seedling establishment

Seedlings are established with a diameter at breast height of 1 cm. Establishment success is simulated as a function of species-specific responses to *DrI*, *GDD*, winter temperature (see Table 1 for species parameter description, and Appendix A), light availability at the forest floor (see Section 2.5) and browsing pressure (Didion et al., 2011). By default, the model assumes that there is a constant seed rain in the patches and thus no dispersal limitation, but alternatively it is possible to activate a feedback between the actual forest composition at year *n* and species composition of the new seedlings at year *n* + 1 (Appendix A).

2.3 | Tree mortality

Tree mortality depends on two components: (a) a 'background' mortality that is constant across time and (b) a growth-related mortality (Appendix A). The background mortality is purely stochastic. It depends on species' maximum longevity and simulates mortality events induced by 'random' small-scale disturbances (e.g. attack of pathogen in an endemic phase). Large-scale disturbances (e.g. windthrows, wildfires) can be taken into account by increasing the background mortality rate, but are not considered here. The growth-related mortality is a proxy for stress conditions, that is, tree mortality probability increases with the decrease in absolute or relative tree growth (i.e. tree vigour) induced by abiotic factors or by competition (DeSoto et al., 2020). It is thus noteworthy that competition has an indirect effect on mortality rates via the growth-related mortality.

2.4 | Potential tree growth

Annual tree growth is modelled through stem diameter increment at breast height (ΔD). Following the classical scheme of gap models, ΔD is calculated in two steps. First, the potential (i.e. maximum)

TABLE 1 Description of the species parameters in ForCEEPS. References refer to the literature used to calibrate all or part of the species for the specific parameter

Parameter	Details	Unit	Example (Fagus sylvatica)	Calibration	References
f_s	Foliage type	Unitless E—evergreen - or D—deciduous and a number between 1 and 5	D3	Literature	Rameau et al. (1989) and Didion et al. (2009)
H_{max_s}	Maximum height	m	50	Literature + NFI	Rameau et al. (1989, 2008)
s_s	Allometry	Unitless	76	Literature + NFI	Didion et al. (2009)
g_s	Optimal growth rate	Unitless	260	Literature + NFI	Didion et al. (2009)
A_{max_s}	Maximum age	years	400	Literature	Rameau et al. (1989) and Bugmann (1994)
DD_{min_s}	Minimal required annual or seasonal degree-days sum	°C	841	Literature	San-Miguel-Ayanz et al. (2016)
$DrTol_s$	Drought tolerance index, to be compared to the evapotranspiration deficit based on a bucket model of soil moisture	Continuous index with values between 0 (sensitive) to 1 (tolerant)	0.25	Literature	Ellenberg and Mueller-Dombois (1966), Niinemets and Valladares (2006) and Rameau et al. (1989, 2008)
$NReq_s$	Soil nitrogen requirement	Integer Index with values between 1 (weak requirements) to 5 (strong req.)	2	Literature	Ellenberg and Mueller-Dombois (1966) and Bugmann (1994)
$ShTol_s$	Shade tolerance	Integer index with values between 1 (shade tolerant) to 9 (shade intolerant)	1	Literature	Ellenberg and Mueller-Dombois (1966), Niinemets and Valladares (2006) and Rameau et al. (1989, 2008)
$ShTol\_seedling_s$	Shade tolerance of seedlings, to be compared to the relative amount of light reaching the ground	Continuous index with values between 0 (tolerant) to 1 (sensitive)	0.05	Literature	Ellenberg and Mueller-Dombois (1966), Niinemets and Valladares (2006) and Rameau et al. (1989, 2008)
WT_{min_s}	Monthly minimum winter temperature tolerated for regeneration (°C)	°C	−6	Literature	Didion et al. (2009) and San-Miguel-Ayanz et al. (2016)
WT_{max_s}	Monthly maximum winter temperature tolerated for regeneration	°C	9	Literature	Didion et al. (2009) and San-Miguel-Ayanz et al. (2016)
Br_s	Browsing susceptibility of seedlings	Integer index with values between 1 (less susceptible) to 5 (more susceptible)	3	Literature	Didion et al. (2009)

diameter increment (ΔD_{opt}) of each tree is predicted in each year using the following empirical equation (Moore, 1989):

$$\Delta D_{opt} = g_s \frac{D\left(1 - \frac{H}{H_{max_s}}\right)}{2.H_{max_s} - b_S \times e^{(c_s.D)\times(c_s.D+2)}}, \quad (1)$$

where D is the tree diameter at breast height, H is the tree height, g_s is the maximum growth rate of species s, H_{max_s} is the maximum height reachable by the species s, and b_s and c_s are species-specific parameters (with $b_s = H_{max_s} - 137$; and $c_s = S_s/b_s$); s_s is a species-specific allometric parameter relating tree height and diameter as follows (Bugmann, 1996):

$$H = a + \left(H_{max_s} - a\right) \times \left(1 - e^{\left(\frac{-S_s.D}{H_{max_s} - a}\right)}\right), \quad (2)$$

with $a = 1.37$ m (i.e. breast height). Therefore, simulating the potential diameter increment of a tree in ForCEEPS requires to determine the values of the species-specific parameters g_s, s_s and H_{max_s} (Table 1).

2.5 | Realized tree growth

Realized tree diameter increment ΔD is calculated by modifying ΔD_{opt} according to abiotic or biotic growth reduction factors (all

factors are bounded between 0 and 1) following a modified geometric mean (Bugmann, 1996; Didion et al., 2009):

$$\Delta D = \Delta D_{\text{opt}} \times \sqrt[3]{\text{GR}_{\text{light}} \times \text{GR}_{\text{gdd}} \times \text{GR}_{\text{drought}} \times \text{GR}_{\text{soil}}}, \quad (3)$$

where GR_{light} is the growth reduction factor related to light availability for the tree, GR_{gdd} is the growth reduction factor related to growing season temperatures of the site (GDD), $\text{GR}_{\text{drought}}$ is the growth reduction factor related to the site drought index (DrI) and GR_{soil} is the growth reduction factor related to soil nutrients content (N_{soil}; see Appendix A). The effects of each of these growth reduction factors on realized tree growth depend on species-specific parameters: GR_{light} depends on species shade tolerance ShT_s; GR_{gdd} depends on species minimum sum of growing degree-days DD_{min_s}; $\text{GRR}_{\text{drought}}$ depends on species drought tolerance DrT_s; and GR_{soil} depends on species requirements for soil nutrients NReq_s (see Table 1). All growth reduction factors vary among site conditions and species, and GR_{light} varies also among trees because it is influenced by the sizes of the neighbouring trees in the patch (see next section).

2.6 | Effects of the competition for light on tree growth

In ForClim 2.9.6 (Didion et al., 2009), the amount of light available for a tree (with H being its total height) is reduced by the leaf area of the trees found in the same patch whose height is greater than H or equal to H. Thus, all the foliage of trees taller than the target tree contribute to the shading. A major originality of ForCEEPS is that it embeds a more realistic description of the competition for light, by representing individual crown lengths in the vertical space of the canopy (Figure S1 and Appendix A).

In ForCEEPS, the growth reduction factor related to light availability (GR_{light}) has two components:

$$\text{GR}_{\text{light}} = \text{GR}_{\text{cs}} \times \text{GR}_{\text{sh}}, \quad (4)$$

with GR_{cs} representing the feedback of crown size on tree growth, that is, tree leaf area is positively linked to tree growth rate (Mitscherlich & von Gadow, 1968). GR_{sh} is the reduction factor related to shading by competing trees. The key feature is that individual tree crowns are characterized by crown length cl, calculated as follows for each tree i:

$$\text{cl}_i = \text{cs}_i \times H_i, \quad (5)$$

with H being tree height and cs being the ratio of the height with green crown, which is related to light exposition of the tree (Didion et al., 2009). For each tree, cs varies between two extreme species-specific values that represent the case where the tree is fully shaded ($\text{cs} = \text{cs}_{\text{min}_s}$) or in full light ($\text{cs} = \text{cs}_{\text{max}_s}$), with:

$$\text{cs}_i = \text{cs}_{\text{max}_s} - \left(\text{cs}_{\text{max}_s} - \text{cs}_{\text{min}_s}\right) \times k_{\text{LA}_i}, \quad (6)$$

where the extreme values cs_{max_s} and cs_{min_s} have been derived from the relationship between foliage fresh weight and DBH described in Wehrli et al. (2007) and depends on the foliage type parameter f_S (see Appendix A and Table C in this appendix), and k_{LAI} is the correction factor—ranging from 0 (no shading) to 1 (full shading)—calculated by Didion et al. (2009) as follows:

$$k_{\text{LAI}_i} = \min\left[\left(\frac{\text{LAI}_{H_i}}{\text{LAI}_{\text{max}}}\right)^2, 1\right], \quad (7)$$

with LAI_H being the cumulative double-sided leaf area index between the top of the canopy and the top of the target tree (i.e. between the top of the canopy and the height H) and LAI_{max} being the maximum value of double-sided leaf area index in a patch, resulting from the light compensation point of the most shade-tolerant European tree species (i.e. $\text{LAI}_{\text{max}} = 11.98$; Bugmann, 1994, Didion et al., 2009).

The vertical space of the patch p at simulation step $t = t_1$ is discretized in $n(p, t_1)$ layers of a given width w, whose value is bounded between 0 (ground level) and $H_{\text{max}}\left(p, t_1\right)$ (height of the tallest tree in the patch p at $t = t_1$), with $w = 1$ m. We assumed that tree leaf area decreases linearly from the top to the base of the crown, that is, from the highest to the lowest layer in which the crown of the tree is found (Figure S1b; Eermak, 1998; Van Pelt et al., 2016). We are aware that tree crown shape and vertical leaf area distribution vary among tree species and are also affected by the size and identity of neighbouring trees (Niklaus et al., 2017; Poorter et al., 2006; Williams et al., 2017). Our assumption should thus be seen as a first parsimonious step that can be refined using species- and context-specific architectural data. Further details about the calculation of GR_{cs} and GR_{sh} are described in Appendix A.

2.7 | Effects of the environmental conditions on tree growth

Below-ground competition for water and nutrients is not explicit in ForCEEPS. Although the model focuses on competition for light in its current version, it is noteworthy that soil nutrient content and soil moisture indirectly affect competition for light, in a way that differs among species (Table 1). In fact, GR_{soil} and $\text{GR}_{\text{drought}}$ affect tree dimensions (diameter and height; Equation 3) and thus tree leaf area, which, in turn, modifies the competitive ability of a tree because shading directly depends on leaf area (Appendix A, Equations 27 and 28). Therefore, site conditions (soil and climate) modulate competition among trees.

The model is available on the CAPSIS modelling platform (Dufour-Kowalski et al., 2012).

3 | PARAMETERIZATION, VALIDATION AND SENSITIVITY ANALYSIS

3.1 | Species

The parameterization and validation of ForCEEPS were done for nine species (Table S1)—four Angiosperm species and five Gymnosperm

species, including the seven most widespread tree species in France (*Quercus petraea*, *Q. robur*, *Fagus sylvatica*, *Abies alba*, *Picea abies*, *Pinus sylvestris* and *P. pinaster*; IGN, 2018), and two main species of Mediterranean French forests (*Pinus halepensis* and *Quercus ilex*). Furthermore, *P. pinaster* is the planted species covering the largest area in France. These species dominate in contrasted stages of the vegetation succession: pioneer (*Pinus*), intermediate- (*Picea*) or late-succession species (*Quercus*, *Fagus*, *Abies*).

Furthermore, for the PNV simulations, we complemented the set of studied species by considering 13 additional species ('*other species*' in Table S1) to cover most possible forest types: *Acer campestre*, *A. platanoides* and *A. pseudoplatanus* (grouped in '*Acer*' species); *Larix decidua* and *Pinus cembra* (grouped in '*mountain gymnosperms*'); *Sorbus aria*, *S. aucuparia and Ulmus glabra* (grouped in '*mountain broadleaves*'); *Betula pendula*, *Fraxinus excelsior* and *Populus tremula* (grouped in '*other broadleaves*' species); *Carpinus betulus* and *Quercus pubescens*. However, no forest growth data were available to properly calibrate or validate the model for these other species as done for the nine main ones. This notably occurred because growth data at the stand scale were not available for these species (see Validation section) and growth data at the tree scale were only available for *C. betulus* and *Q. pubescens* (see Table S2).

The workflow of the study is summarized in Figure 2.

3.2 | Parameterization

Each species simulated in ForCEEPS is defined by 13 key parameters described in Table 1 (and Table S1) from which other parameters were derived (b_s and c_s in Equation 1, cs_{min_s}, cs_{max_s} in Equation 6, f_s, a_s, and LCP_s in Appendix A). The variability among functional traits reflects fundamental trade-offs of species life-history strategies (Bazzaz, 1979; Violle et al., 2007). In ForCEEPS, like in many gap models, the variability among parameters' values aims at reflecting such trade-offs (Bugmann, 2001), and in this sense we further assume that the parameters describing the species in the model are proxies of life-history or functional traits. For instance, late-successional species are generally characterized by slow growth (i.e. low values of g_s), long lifespan (i.e. low values of A_{max_s}) and high shade tolerance (i.e. low values of $ShTol_s$), in contrast to early-successional ones (Reich, 2014).

In the present study, the parameterization of potential tree growth (i.e. species-specific parameters g_s and H_{max_s}) and the allometry relating tree height and diameter (i.e. parameter s_s) were based on data from the French National Forest Inventory (NFI) (IGN, 2018). The values of other parameters were based on the literature. The NFI sampling design warrants an exhaustive representation of environmental gradients within the realized distribution of the species over the mainland French territory while individual plots may not be

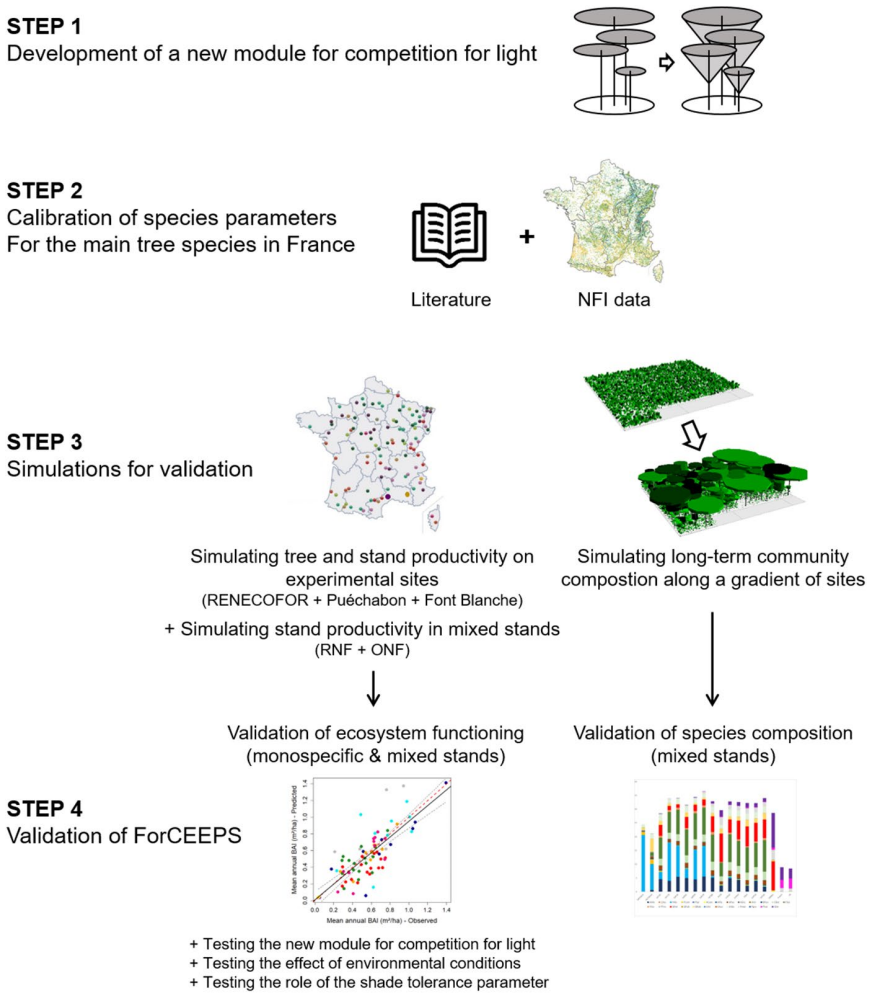

FIGURE 2 Summary of the workflow of the study. This figure illustrates the sequence of the main steps of the study

locally representative (Charru et al., 2010). Therefore, we used NFI to calibrate the potential growth model in ForCEEPS, but did not use it for the validation at the plot level. More detailed information about NFI data is available in Appendix D.

Parameter g_s. This parameter is the most difficult to calibrate as it requires data from trees growing in 'optimal conditions', which are scarce in observational datasets as the growth of trees is usually constrained by environmental conditions or biotic factors (e.g. competition). To cope with this challenge, we took advantage of the NFI that covers a very wide range of conditions (in both space and time), providing a large number of 'annual diameter increment versus diameter' pairs for each of the 11 species (i.e. the nine main species and *C. betulus* and *Q. pubescens*) for which abundant data were available (n = 206,569 for all species confounded, Table S2). For each of these 11 species, we grouped trees according to their diameter (according to 1-cm size classes) and selected the 10% of trees with the greatest annual diameter increment, assuming that these trees grew in 'optimal conditions' or at least under almost unconstrained conditions. However, we note that the annual increments are derived from 5-year average, which may lead to an underestimation of the actual greatest annual diameter increments. Then we fitted g_s from Equation 1 with this dataset, using a nonlinear least squares approach implemented by the `nls` function in the R software (R Core Team, 2018). For the remaining species (n = 11), the g_s values have been set from previous studies (Didion et al., 2009).

The fitted values for the parameters g_s ranged from 79 to 399 (Table S1). These values are consistent with former estimates for the same or related species (Bugmann, 1994; Didion et al., 2009).

Parameter s_s. The parameterization of s_s (Equation 2) relied on NFI data because of their representativeness of the conditions in which each species occurs. The whole NFI dataset was used for the parameterization to cover the largest range of conditions in which each species occurs. Although diameter–height relationships were shown to be affected by environmental conditions, for example, climate, tree social status and stand density (Fortin et al., 2019; Trouvé et al., 2015), these factors were not accounted for in the model. The rationale for this lies in our aim to keep the model structure as simple as possible to allow for an easy parameterization and use at large scale for a large number of species. We fitted the height–diameter relationships (Equation 2) on the NFI dataset, using the `nls` R function, and extracted s_s values for each species. As for g_s, this parameterization was conducted for the 11 main species while we relied on Didion et al. (2009) for the 11 additional species.

ParameterH_{max_s}. This parameter was calibrated using NFI data and/or literature (Rameau et al., 1989, 2008) for all the species. Maximum height may indeed be underestimated in the NFI data because forest managers tend to harvest the largest trees before they reach their maximum height.

Other parameters. The values of the parameters describing species' response to abiotic conditions (i.e. effect of the growing season temperature on tree growth, DD_{min_s}; drought tolerance, $DrTol_s$ and soil nitrogen requirement, $NReq_s$), and species intrinsic characteristics (i.e. foliage type, f_s; maximum age, A_{max_s}; shade tolerance, $ShTol_s$; shade tolerance of seedlings, $ShTol\_seedling_s$ and browsing susceptibility of seedlings Br_s) were based on the literature (Table 1 and references therein). Parameters describing the thermal regeneration niche for seedlings (i.e. monthly minimum and maximum winter temperature tolerated for regeneration WT_{min_s} and WT_{max_s}, Table 1) were calibrated according to species-specific diagrams of occurrence (San-Miguel-Ayanz et al., 2016).

3.2.1 | Congruence of key parameter values with functional traits

To gain mechanistic insight into the parameters values derived from the parameterization procedure, we evaluated the congruence of key model parameters with functional traits extracted from the literature. To do so, we first selected the most meaningful ForCEEPS parameters in terms of species ecological strategies, including g_S, $DrTol_S$, $ShTol_S$, $ShTol\_seedling_S$ and $NReq_s$. Then, we collected data on relevant traits from various database, including: xylem cavitation resistance (assess through the water potential causing 50% cavitation, Ψ50 in MPa), leaf turgor loss point (Ψtlp, in MPa), water potential causing stomatal closure (Ψclose, in MPa) and safety margins from Ψtlp and Ψclose (from the SurEAu database; Martin-StPaul et al., 2017), wood density (g/m^3, Chave et al., 2009), light-saturated CO_2 assimilation (or maximal photosynthesis A_{max}, in µmol/m^2/s), nitrogen content per unit leaf area N_a (g/m^2) and leaf mass per area LMA (g/m^2) (from the CANTRIP database; Keenan & Niinemets, 2016). The final trait database and associated references are reported in Appendix E. For each of the selected ForCEEPS parameters, we tested the Pearson's correlations between the ForCEEPS parameters and some of the traits at the interspecific level. Note that the consistence of the results across both Angiosperms and Gymnosperms was taken into account to assess the robustness of the congruence of species parameters with functional traits.

3.3 | Validation against forest growth data

Forest growth dataset. The validation of simulated annual productivity at the tree and stand levels was conducted using a dataset independent from the one used in the parameterization process. Following Guillemot et al. (2017), we primarily relied on the RENECOFOR permanent forest plot network (Ulrich, 1997) that includes 103 half-hectare plots in even-aged managed forests covering most of the main tree species and climate conditions in France. After excluding the plots that had experienced a natural or anthropic disturbance (e.g. thinning) <4 years before the last diameter inventory, 77 plots remained. Most of the stands included in the validation dataset are monospecific or strongly dominated by one species.

The RENECOFOR network does not include forests growing under Mediterranean conditions. Therefore, we completed the validation using data from the long-term experimental sites of Puéchabon (*Quercus ilex*; Rambal et al., 2014) and Font Blanche (mixed forest dominated by *Pinus halepensis*; Simioni et al., 2016). Diameter inventories

were used to estimate the tree and stand basal area increment (BAI) in all validation plots. The time interval between the initial and final inventories in RENECOFOR plots varied between 4 and 14 years, while they were of 14 and 10 years for the Puéchabon and Font Blanche sites, respectively (see further details about the validation datasets in Appendix D). The BAI data recorded over contrasted time intervals were normalized to mean annual BAI. Local measurements of soil water holding capacity (SWHC) were available for all plots, and climate time-series were obtained from the SAFRAN atmospheric reanalysis (Vidal et al., 2010) for the RENECOFOR plots, and from on-site measurements for the Puéchabon and Font Blanche plots. The validation plots covered a large range of environmental conditions, with mean annual temperature (MAT) ranging between 5.8 and 14.3°C, mean annual precipitation sum (MAP) between 700 and 2030 mm, while the drought index ranged from 0.003 to 0.35 (values below 0.05 indicate there is no marked drought stress for the trees, whereas values above 0.3 indicate strong stress for most tree species; Figure S2).

To evaluate the ability of ForCEEPS to simulate forest growth in mixed stands, we used a dataset from 'Réserves Naturelles de France' and 'ONF' (Paillet et al., 2015) that consists in dendrological inventories distributed across French territory, with some plots having been re-measured after a few years. These plots include a 10-m radius circle in which all trees with a DBH comprised between 10 and 30 cm are measured, and a fixed angle plot technique was used to measure the living trees comprised within a fixed relascopic angle of 3%, allowing to sample trees with a DBH > 30 cm at a distance superior to 10 m. This particular technique allows large trees to be more precisely estimated at a small scale. We selected a subset of mixed stands according to the following conditions: (a) plots should have been measured at least twice and 90% of trees should have been re-measured and (b) the dominant species of the plot should not exceed 60% of the plot basal area. We finally selected 18 plots, with nine stands dominated by beech-fir-spruce, five by oaks (*Q. petraea*–*Q. robur*), beech and pine (*P. sylvestris*), three by beech and oaks and one by oaks and *C. betulus* (Table D1 in Appendix D). These plots were mostly located in north-eastern France (Figure D1 in Appendix D). The time interval between initial and final inventories varied between 7 and 11 years. Climate data came from the same source than monospecific plots, and SWHC data have been obtained from European Soil Hydraulic Database (Tóth et al., 2015).

ForCEEPS simulations. We initialized the model for each stand using the first inventory campaign of the respective plot. For each plot, five patches of 1,000 m^2 were simulated, to obtain comparable observed and simulated forest plot areas (the average size of the observed plots is *c.* 5,000 m^2 for RENECOFOR plots and it varies for the mixed stand plots). To simulate the patches, trees were randomly sampled in the inventory dataset of a given plot until the stand basal area per square meter of the simulated patch was comparable to the observed stand basal area per square meter. Local measurements of SWHC and local climate time-series were used as inputs. ForCEEPS simulations were run over the time period for which BAI measurements were available in each plot (i.e. from 4 to 14 years), and subsequently normalized to mean annual BAI. Gap models like ForCEEPS are designed to explore processes occurring at the stand level and are thus more relevant at this scale. However, as neighbourhood interactions are reported to be key in driving BEF relationships and for the sake of comprehensiveness, we also present the results at the tree level for the RENECOFOR plots (Jourdan, Kunstler, et al., 2019; Schnabel et al., 2019). As the results were very consistent across the five repetitions carried out per plot (as shown in Figure S3 for the RENECOFOR plots), we only present the results for one repetition at the tree level for the sake of clarity (the results for each repetition are shown in supplementary material—Table S5a and Figure S3). For results at stand level, we present averages across the five repetitions (the results for each repetition are shown in supplementary material—Table S6a).

3.4 | Quantifying the importance of the hypotheses embodied in ForCEEPS for forest growth

After simulating BAI for each plot using the full model, we carried out three types of simulations to quantify the importance of some hypotheses and ecological processes embedded in ForCEEPS. First, we ran simulations without the new module for competition for light, to test whether an explicit representation of individual crown lengths in the vertical canopy space increased the prediction accuracy of stand growth (*Test 1*). Second, we ran simulations without considering the limiting effect of drought stress and thermal constraints on tree growth, that is, under optimal climatic conditions (*Test 2*). Third, we aimed at testing the importance of the species-specific tolerance to shade in ForCEEPS (*Test 3*), as it has been shown to be a key parameter driving diversity effects in ForClim 2.9.6 (Morin et al., 2011). To do so, we changed the specific values of the parameter $ShTol_S$ by assigning the maximum value to all species. Note that this kind of tests has been rarely done with gap models (but see Huber et al., 2018; Morin et al., 2011).

The performance of the model was assessed using Pearson correlation coefficient (*r*), the root mean square error (RMSE) and the average bias (AB) between observations and model predictions.

3.5 | Validation against potential natural vegetation

Study sites. To validate the model's predictions in terms of outcomes of climate effects and interspecific competition in the long term, we compared the community composition simulated by ForCEEPS with the tree species composing the potential natural vegetation (PNV) along an environmental gradient. Defining PNV for a given site is subject to personal judgement. Here, similarly as in Bugmann (1996), we simply relied on the assumed dominant tree species (assuming no large disturbances) in a space spanned by annual precipitation (MAP) and mean annual temperature (MAT), following Ellenberg (1986), Rameau et al. (1989, 2008) and San-Miguel-Ayanz et al. (2016) (Figure 4b). More precisely, we selected 14 sites with contrasted conditions among the 79 plots used for the validation of forest growth simulations. This gradient thus includes dry and warm conditions through the two Mediterranean sites, but it did not include the

coldest conditions in which forests can grow in France. Therefore, we added another site with average MAT of 2.9°C (±0.64) and ASP of 1,577 mm (±253), corresponding to the conditions of a subalpine site according to Ellenberg (1986) (grey dot in Figure S2, and site 1 in Figure 4b).

ForCEEPS simulations. For each of the 15 sites, we ran 2,500-year simulations, starting from bare ground. Thus, the PNV simulations accounted for seedling establishment, tree growth and mortality. This simulation duration was necessary to avoid the communities to be in a transient phase and to ensure that they reached a pseudo-equilibrium in terms of composition and basal area. The 2,500-year climate time-series were obtained by randomizing the years from which time series were available for each site. In other words, we considered inter-annual variability in climate, but there was no trend in the long term, as commonly done in studies aiming at depicting forest succession with gap models (e.g. Bugmann, 1996; Chauvet et al., 2017; Morin et al., 2011). We considered 200 patches of 1,000 m^2 for each simulation. At the end of the simulation, we extracted the mean basal area per hectare of the simulated stands and the basal area of each species.

4 | RESULTS

4.1 | Prediction of above-ground tree growth

ForCEEPS was able to capture the observed mean annual BAI (Figure 3) at the tree level, with a good correlation between observations and predictions (r = 0.72, n = 2,662; Table S4) while the difference between observations and predictions was satisfactory (RMSE = 0.0012, AB = 12.4%). There was, however, a slight tendency to underestimate the growth of the most productive trees (Figure 3), and the uncertainty of the model predictions increased with tree diameter (Figure S6). When the species were examined separately, the Pearson correlation coefficient ranged from 0.49 (*P. sylvestris*) to 0.77 (*F. sylvatica*) (Table S4, Figure S4) but the difference between observations and predictions strongly varies between species (RMSE = 0.0013 and AB = 21.8%, on average).

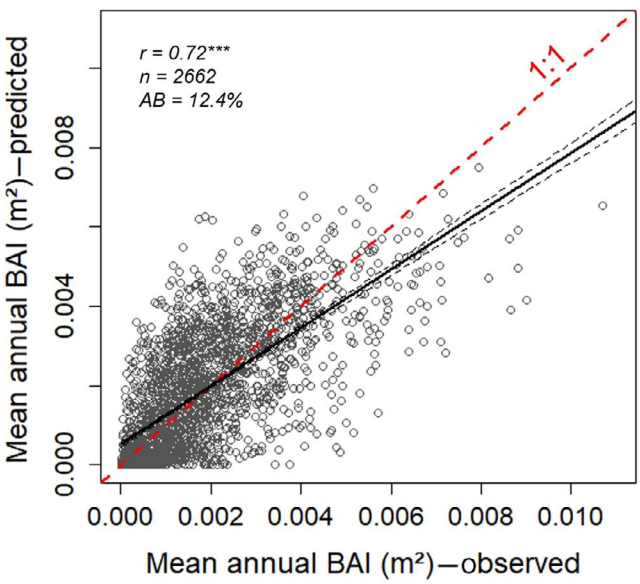

FIGURE 3 Predicted (by ForCEEPS) against observed mean annual tree basal area increment (BAI) for all considered trees (over 82 sites) and one repetition. The plain black line is the regression line of the linear model of the relationship between observed and predicted tree growth, with confidence interval represented with the grey dashed lines; the dashed red line is the 1:1 line. Statistics associated: see Table S4

4.2 | Prediction of above-ground stand growth

At the stand level, ForCEEPS showed a good ability to reproduce observed mean annual BAI regardless of the species or the environmental conditions. Across all plots, the correlation was strong between observations and predictions (r = 0.79, p < 0.001, Tables S6 and S7) with a very low difference between observations and predictions (RMSE = 0.019 and AB = 4.5%—Figure 4a, Table S7) without strong bias related to the basal area of the stand (Figure S7). When species were examined separately, the accuracy varied across species, but the results did not show strong systematic bias (Figure S5, RMSE = 0.014 and AB = 26.7% on average, Table S7b) except for *Q. petraea*, for which productivity of the most productive plots was underestimated (RMSE = 0.016 and AB = −16.7%, Figure S5), and *P. pinaster*, which showed the highest variability (RMSE = 0.034 and AB = 50.3%, but it is the species with the smallest number of observations—except *Q. ilex* and *P. halepensis* for which one can hardly make any conclusion with only three plots).

Regarding the simulations for mixed stands, ForCEEPS also showed a good ability to reproduce observed mean annual BAI regardless of the species composition or the environmental conditions. Across all plots, the correlation was strong between observations and predictions (r = 0.75 on average, Table S8), with a very low difference between observations and predictions (AB = 3.8% and RMSE = 0.09 on average—Table S8, Figure 5a). When focusing the analysis only on the main species of the study (Table S8), the correlation was even stronger, also the average bias increased (Figure 5b).

4.3 | The importance of light competition, environmental conditions and shade tolerance for simulating forest growth in ForCEEPS

4.3.1 | Testing the representation of light competition

The new module for competition for light, which include an explicit representation of individual crown lengths in the vertical canopy space, yielded on average better results than the former

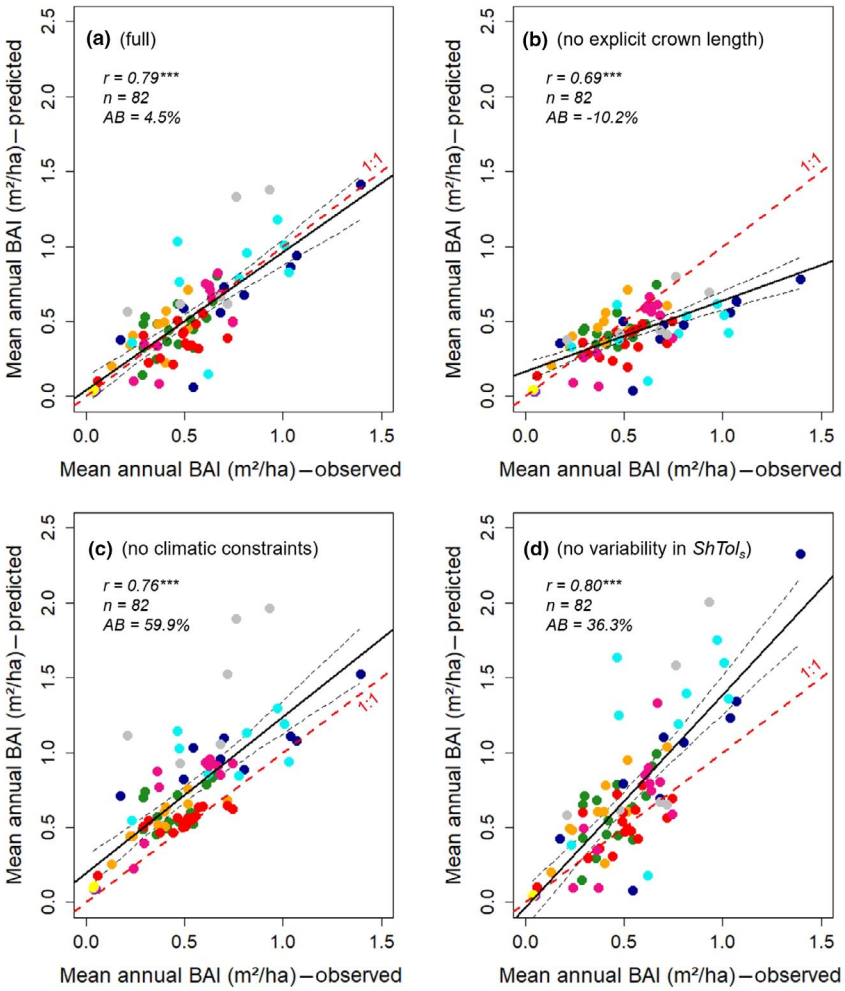

FIGURE 4 Predicted (by ForCEEPS) against observed mean annual stand basal area increment (BAI) for the 82 sites, using different model configurations: (a) ForCEEPS simulations with the new crown length module, climatic constraints on tree growth and interspecific variability in shade tolerance (parameter $ShTol_s$). (b) ForCEEPS simulations without the new crown length module. (c) ForCEEPS simulations without climatic constraints on tree growth. (d) ForCEEPS simulations without interspecific variability in parameter $ShTol_s$. For all panels: the plain black line is the regression line of the linear model of the relationship between observed and predicted stand productivity, with confidence interval represented with the grey dashed lines; the dashed red line is the 1:1 line. Statistics associated: see Table S7a. Colour code for the species as follows: ●, *Fagus sylvatica*; ●, *Quercus robur*; ●, *Quercus petraea*; ●, *Quercus ilex*; ●, *Abies alba*; ●, *Picea abies*; ●, *Pinus sylvestris*; ●, *Pinus pinaster*; ●, *Pinus halepensis*

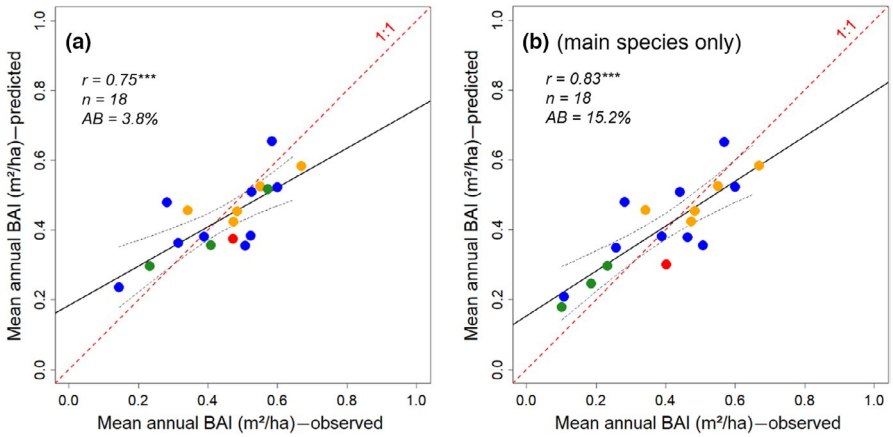

FIGURE 5 Predicted (by ForCEEPS) against observed mean annual stand basal area increment (BAI) for the 18 sites with mixed stands, with all species (panel a) or only the nine main species (panel b, see Table S1). For all panels: the plain black line is the regression line of the linear model of the relationship between observed and predicted stand productivity, with confidence interval represented with the grey dashed lines; the dashed red line is the 1:1 line. Statistics associated: see Table S8. Colour code for the stand composition (dominant species in terms of basal area) as follows: ●, *Abies alba/Fagus sylvatica/Picea abies*; ●, *Quercus petraea/Quercus robur/Fagus sylvatica/Pinus sylvestris*; ●, *Fagus sylvatica/Quercus petraea/Quercus robur*; ●, *Quercus petraea/Quercus robur/Carpinus betulus*

version (decrease by 15.4% in RMSE; Table S7a). The former version tended to underestimate the productivity of the most productive plots while this was not the case with the new version (Figure 4a,b).

4.3.2 | Testing the effect of environmental conditions

The model without climatic constraints on tree growth was less accurate than the full version (increase by 69.7% in RMSE; Figure 4a,c; Table S7a),

except for a few plots—especially for *Q. petraea* stands. The simulations without climatic constraints logically tended to overestimate stand productivity (Figure 4c). It is thus noticeable that on average, the effect of climatic conditions improved the accuracy of the simulations over such a large range of environmental conditions tested in this study (illustrated in Figure S2). One may also notice that this improved accuracy is consistent across species, regardless their averaged productivity.

4.3.3 | Testing the importance of the variability in the shade tolerance parameter

When the variability in the ability of species to tolerate shade was not taken into account in ForCEEPS, the model's performance strongly decreased, with an increase in RMSE by 85.11% across plots (Figure 4a,d; Table S7a). The bias notably increased for the most productive stands, especially dominated by *A. alba* and *P. abies* (Figure 4d).

4.4 | Prediction of species composition in the long term

When comparing the distribution of the dominant tree species at the end of the 2,500-year simulations carried out along the environmental gradient covered by the 15 sites (Figure 6), it appeared that the ability of ForCEEPS to predict reliable PNV varied across sites: the overall likelihood of the simulated communities is strong, but with a greater uncertainty about Mediterranean forest types.

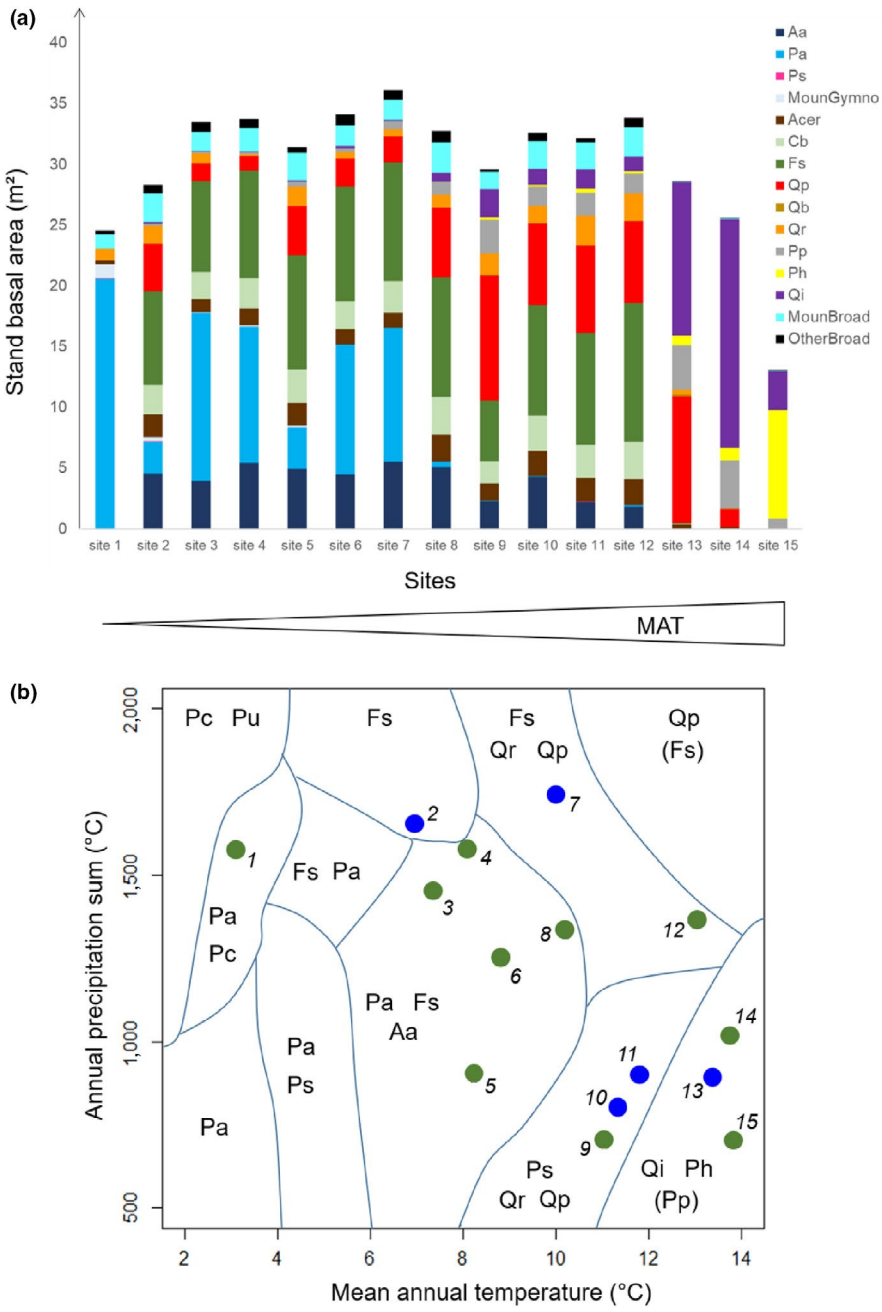

FIGURE 6 (a) Simulated basal area (m^2/ha) at the end of long-term ForCEEPS simulations along sites representing a gradient of environmental conditions from cold and moist alpine conditions (left) to warm–dry Mediterranean conditions (right). The site names and conditions are stated in Table S3, with Aa (*A. alba*); Pa (*P. abies*); Ps (*P. sylvestris*); Cb (*C. betulus*); Fs (*F. sylvatica*); Qp (*Q. petraea*); Qb (*Q. pubescens*); Qr (*Q. robur*); Pp (*P. pinaster*); Ph (*P. halepensis*); Qi (*Q. ilex*); MounGymno (mountainous gymnosperm species including *L. decidua* and *P. cembra*); MounBroad (mountainous broadleaf species including *S. aria*, *S. aucuparia* and *U. glabra*); OtherBroad (broadleaf species including *B. pendula*, *F. excelsior* and *P. tremula*). (b) Distribution of the 15 tested sites in the PNV diagram of the supposed dominating species (built according to mean annual temperature and annual precipitation sum). Green dots: sites for which the dominating species in the simulated communities were accurately predicted according to the PNV diagram; Blue dots: sites for which at least one of the dominating species was accurately predicted but with another dominating species not supposed to dominate according to PNV diagram. Red dots: sites in which the simulated community was dominated by other species than supposed by the PNV diagram. Numbers refer to the site number (see Table S3). PNV dominating species are Pc (*P. cembra*), Pu (*P. uncinata*); Aa (*A. alba*); Pa (*P. abies*); Fs (*F. sylvatica*); Qp (*Q. petraea*); Qr (*Q. robur*); Pp (*P. pinaster*); Ph (*P. halepensis*); Qi (*Q. ilex*)

In 10 out of the 15 sites, the dominating species were accurately predicted according to the PNV diagram (green dots in Figure 6b). In the five other sites, at least one of the dominating species was accurately predicted (blue dots in Figure 6b) while there was no site in which the simulated community was dominated by species other than those expected.

Long-term simulation of stand basal area cannot be directly evaluated against field observations as there are no forest stands unaffected by management for several centuries at these sites. Yet, one may notice that the values appear consistent (albeit a bit low) with mature stands, and that the simulated basal area was lower in the harshest conditions (i.e. at both extremes of the gradient). However, the basal area for the Font Blanche site seemed to be underestimated (*c*. 15 m^2; Simioni et al., 2016).

It is noticeable that the cumulated basal area of the species that were not validated against forest growth data in the present study (i.e. the 'other species' in Table S1) represents on average only 17% (across the 15 sites) of stand basal area at the end of the simulations, and it remains below 25% at all sites.

4.5 | Congruence of key parameter values with functional traits

We found correlations between traits and ForCEEPS parameters, but their sign and significance strongly varied. The species nitrogen requirement $NReq_s$ was found to correlate with N_a (Table S9). The growth parameter g_S was significantly negatively correlated with wood density (Figure 7), while the correlation with LMA was not consistent for Angiosperms and Gymnosperms (Table S9). Seedling and adult shade tolerance were correlated with light-saturated photosynthesis (A_{max}, Figure 7 and Table S9). Other traits, including LMA and wood density, were poorly correlated with shade tolerance. Finally, correlations were found between $DrTol_S$ and different drought-related functional traits. In particular, a strong correlation was found between $DrTol_S$ and the stem xylem embolism resistance (assessed by *P*50, i.e. the water potential causing 50% embolism, Figure 7). The correlation between $DrTol_S$ and *P*50 was very strong for angiosperms ($r^2 = 0.7$, $p < 0.001$) but not significant for gymnosperms ($p = 0.1$), which could be explained by the fact that the studied conifers all belong to the *Pinaceae* family that rely on a tight stomatal control of transpiration during drought (Brodribb et al., 2014). Positive but less pronounced relationships were found between $DrTol_S$ and the turgor loss point (Table S9). $DrTol_S$ was also correlated with wood density and LMA but to a lower extent (Table S9).

5 | DISCUSSION

5.1 | A gap model predicting annual productivity and community composition

ForCEEPS relies on ecological hypotheses, notably the trade-off between maximum growth and tolerance to competition (Rees et al., 2001) and the fact that cyclical succession is occurring in each individual patch (Botkin et al., 1972), allowing to simulate long-term species ecological succession. Although most biogeochemical processes are implicit in the model, as in most gap models, our results show that ForCEEPS accurately predicts both the dominant species occurring at a site in the long term and the wood productivity of monospecific stands across a few years.

Gap models have long demonstrated their ability in predicting the long-term dominant species of forests (Bugmann, 2001), but it is noticeable that ForCEEPS appeared robust across a large range of environmental conditions, that is, from alpine to Mediterranean forests. Indeed, if gap models were already shown to accurately predict dominant species composition in temperate and subalpine forests (e.g. Bugmann, 1996; Didion et al., 2009), the good performances of ForCEEPS at Mediterranean sites appear as a major achievement. Although this validation remains mostly qualitative (and the use of PNV relies on expert knowledge), the accuracy of predicted community composition from the long-term simulations is noticeable, and suggests that the interspecific competition and

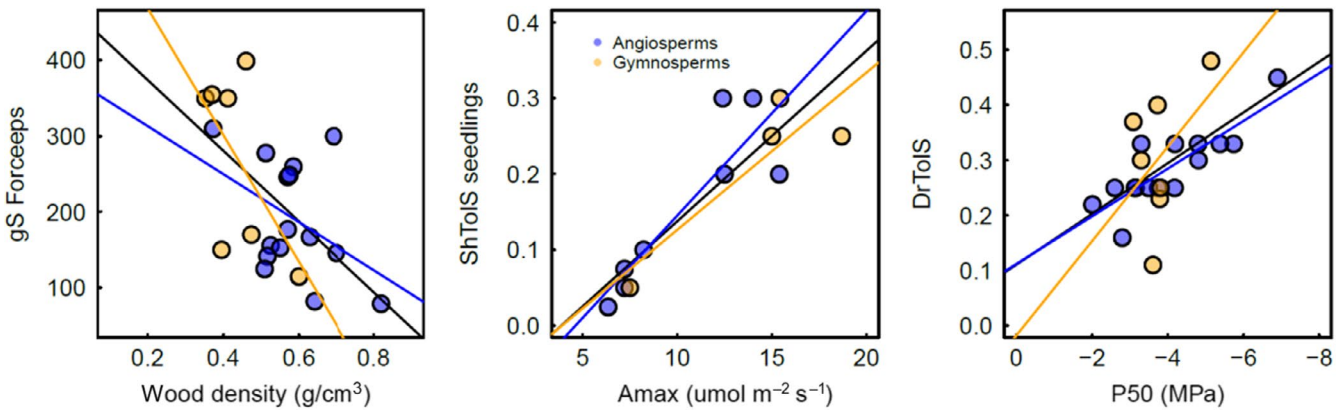

FIGURE 7 Correlations between key ForCEEPS parameters and ecophysiological traits extracted from the literature (see Appendix E). Blue dotsand line: Angiosperms; orange dots and line: Gymnosperms. Associated statistics are presented in Table S9

abiotic constraints are well represented in ForCEEPS. The good performances of ForCEEPS across large environmental gradients and for the most important tree species found in mainland France suggest that the model could be applied to a large part of the European forest ecosystems.

The validation of the ability of ForCEEPS to predict forest functioning in the short term (i.e. across a few years) was conducted using forest growth data, focusing primarily on monospecific stands. The rationale for this choice was to evaluate its behaviour and predictive ability in a context with low influence of complex interspecific interactions. Because gap models are often validated using species composition of PNV at selected sites, their validation is actually conducted in mixed forests in most cases (Bugmann, 2001). Thus, this test of the ability of gap models to accurately simulate the functioning of monospecific stands in various environmental conditions and for a wide range of species (Fig. 4a) has been very rarely assessed. Yet, monocultures are often compared to mixed stands to quantify biodiversity effects in forests (e.g. as in Morin et al., 2011). Ensuring that the functioning of monospecific stands is well reproduced by a gap model is thus a *sine qua non* condition to simulate non-biased biodiversity effects in tree communities. Furthermore, although reliable forest growth data from mixed stands growth were scarcer in the study region, we nevertheless checked here that the model's predictions were also robust for mixed stands. The results showed that ForCEEPS was indeed able to reproduce mean annual productivity with a good accuracy and for various kinds of mixed stands, with an average bias similar to monospecific stands. Yet, the RMSE was slightly higher than for monospecific stands, which can be related to the fact that the mixed stands included other species than the nine main ones (i.e. for which the model has been properly parameterized in this study—Table S1), possibly altering the quality of predictions. More generally, validation against forest growth data was rarely done for gap models (Bohn et al., 2014), especially for such a wide range of species and conditions. Gap models have not originally been designed to work at short temporal scales, and are thus not expected to accurately simulate annual tree or stand growth (Fyllas et al., 2014; Mette et al., 2009). Although ForCEEPS may never offer detailed mechanistic insights into ecosystem biogeochemistry and tree growth as ecophysiological models do (Dufrêne et al., 2005; Guillemot et al., 2017; Makela et al., 2000), it can nevertheless be considered as a parsimonious alternative—notably in terms of calibration effort—to explore how productivity will respond to changes in species composition and climate.

Recent advances in forest ecology have resulted in physiological process-based models that can be fully parameterized (e.g. Maréchaux & Chave, 2017; Martin-StPaul et al., 2017) using functional traits available from global databases (Kattge et al., 2011). Although these models provide a unique insight on the physiological mechanism driving forest growth and survival, they are not aimed to describe the long-term ecological processes shaping forest composition on the long term. In this study, we evidence that the processes embodied in gap models to simulate long-term forest succession can also predict annual forest growth in species with contrasted ecology and under various climate conditions, making them an important tool to study forest responses to climate change. ForCEEPS requires a rather small number of parameters to describe a species, allowing both a straightforward parameterization of some parameters using forest inventory data and an a priori parameterization of the other parameters relying on literature and ecological knowledge. Consequently, the hypotheses embodied in ForCEEPS regarding the complex feedback loops and threshold mechanisms that drive forest functioning and forest community dynamics can be conceptualized, parameterized and evaluated against measured field data. This limits the uncertainty that can affect model predictions in case of equifinality. Of course, ForCEEPS—like all gap models—could also greatly benefit from the current increasing availability of forest inventory data to improve its calibration using inverse modelling approaches (Hartig et al., 2012).

5.2 | Hypotheses, limitations and future directions to improve the model

The high accuracy of ForCEEPS in predicting mean annual stand productivity of forests over a few years thus opens good perspectives for ecological studies. However, this potential should not conceal the simplifications and limits of our approach. Our results showed that explicitly representing 2D competition for light by considering crown size in the vertical canopy space improved the accuracy of the predictions of short-term productivity compared to the 'classic' scheme of gap models (Bugmann, 2001). Meanwhile, the reliability of the model's predictions of community composition and standing biomass in the long term still appears valid with this novel development. Yet, introducing this change in the model implied to make some assumptions on crown traits and foliage distribution in vertical space. There is an increasing number of studies showing that these properties vary depending on species identity (Bayer et al., 2013; Forrester & Albrecht, 2014; Forrester et al., 2018), and the size and identity of neighbouring trees (Niklaus et al., 2017; Poorter et al., 2006; Williams et al., 2017). While future work may further improve the representation of canopy space exploration by taking into account the plasticity of tree branching patterns, we believe that the current version of the model relies on a sufficiently parsimonious approach to explore new questions regarding above-ground tree–tree interactions in mixed stands. Keeping track of tree coordinates in horizontal space—as already done in other models (Bohn et al., 2014; Maréchaux & Chave, 2017)—would allow to more finely tackle the mechanism driving tree interactions, but this may come at the cost of finding relevant data for a large number of species and probably increasing the simulation time.

We demonstrate in this study that both the climatic constraints and the variability in species' shade tolerances are crucial to predict short-term productivity with gap models. In particular, we showed that differences in shade tolerance among species are key community features driving diverse forest productivity, which has not been shown across such a wide environmental gradient to our knowledge (Toïgo et al., 2018; Van de Peer et al., 2018). In turn,

this reinforces the need for further exploration of light-mediated tree interactions to understand the mechanisms driving species assemblage and productivity in mixed forests. Although these quantifications are necessarily related to the way the climatic growth-reducing factors and competition for light are modelled, they nevertheless provide an a posteriori justification of the processes embedded in these models. This also confirms the large potential of such models for exploring how diversity affects forest functioning (Cordonnier, Bourdier, et al., 2018; Toïgo et al., 2018; Van de Peer et al., 2018) and how climate change is mediating this effect (Morin et al., 2018).

Yet, this study considered short-term growth, that is, tree or stand growth averaged across a few years. Testing the performance of ForCEEPS on actual annual data of tree and stand increments would have constituted an even stronger test. However, this kind of data is rarely available for all trees on ~1,000 m^2 plots (see Nehrbass-Ahles et al., 2014), especially for large number of species and range of environmental conditions.

For the sake of generality, ForCEEPS relies on generic DBH–height relationships, although these relationships are known to change with tree age and tree density (Fortin et al., 2019; Trouvé et al., 2015). Improvements in this direction may be possible, even though calibrating this allometric parameter would require more detailed inventory data (Rasche et al., 2012), and may have a very limited effect on the model's results when compared to the effect of other parameters (see sensitivity analysis of the ForCLIM model by Huber et al., 2018 and Morin et al., 2011).

More generally about long-term predictions, reaching stronger robustness in predicting long-term species coexistence and community composition would necessitate to better model the occurrence of mortality events and regeneration. In fact, improving the representation of these two processes is a main challenge in forest modelling, especially to better assess climate change impacts on forest functioning (e.g. for mortality; Bugmann et al., 2019; Cailleret et al., 2017; Hülsmann et al., 2018; Vanoni et al., 2019). Besides, although nutrients and water content in the soil indirectly affect competition between trees (see Methods section), future developments may lead to a multi-dimensional competition along several niche axes (Speich et al., 2020). One may also notice that the results for the two Mediterranean sites presented here are already satisfying. Furthermore, the impacts of abiotic (e.g. fire, extreme drought events) and biotic (e.g. pathogens, herbivory) interacting disturbances are also key factors that should be better considered by these models in the future (Seidl et al., 2017).

5.3 | Mechanistic relevance of ForCEEPS parameters

The analysis exploring the congruence between key ForCEEPS' parameters and functional traits retrieved from the literature aimed at highlighting to what extent the parameters describing species in ForCEEPS can be linked to their ecophysiology. First, the negative correlation between the growth parameter (g_S) and wood density appears meaningful as wood density describes the carbon investment per unit volume of stem (Chave et al., 2009), thus indicating that fast-growing species favoured wood volume (i.e. space exploration) at the expense of wood resistance to mechanical or biotic damages.

Shade tolerance is one of the features that segregate ecological groups of tree species and that explain BEF patterns in forests. Some studies indicate that shade tolerance is related to a combination of structural properties maximizing leaf area per unit of respiring biomass, and to a combination of leaf properties optimizing photosynthesis per unit of nitrogen investment. In particular, shade-intolerant or pioneer species are frequently thought to display higher light-saturated net photosynthesis (*A*max) than shade-tolerant or late successional species (Coste et al., 2005; Reich & Walters, 1994). Consistent with this later assertion, we found a significant and consistent correlation between ShTol_seedling_S and A_{max} (Figure 5), and to a lower extent between ShTol_S and A_{max} (Table S9). However, no correlation was found with LMA, which echoes the debate regarding the multiple factors influencing this trait—including ontogeny, leaf life span and light environment—that can blur any expected pattern (Lusk & Warton, 2007).

Drought tolerance (DrTol_S) is another key parameter that was positively correlated with a number of functional traits (Table S9, Figure 5). The best correlation, however, was found with species embolism resistance (assessed through the water potential causing 50% loss of conductivity, *P*50). This pattern is consistent with current ecophysiological knowledge that xylem embolism is a key driver of species mortality during drought (Adams et al., 2017; Martin-StPaul et al., 2017). Additionally, a significant but weaker correlation was found between DrTol_S and the turgor loss point—a trait linked to the maintenance of leaf hydration and functions at low water potential (Bartlett et al., 2012) and to stomatal control (Brodribb & Holbrook, 2003; Martin-StPaul et al., 2017). This lower correlation is consistent with the fact that the variability of turgor loss point is much more constrained among plants than the *P*50 (Martin-StPaul et al., 2017). Such strategy, constrained by the phylogenetic lineage, strongly contributes to drought tolerance, and might thus have limited need to develop a water transport system resistant to cavitation (i.e. lower P50) for drought-tolerant species (such as *Pinus halepensis*).

Interestingly, as for ShTol_S, DrTol_S was only weakly correlated with wood density and LMA, which is probably related to their poor mechanistic relevance in the species resistance to drought (Bartlett et al., 2012; Chave et al., 2009).

Although performed on a relatively small number of species, these results nevertheless pave the way for potential improvement of the representation of drought tolerance in ForCEEPS, for instance by implementing an hydraulic failure module that mechanistically integrate multiple traits (e.g. Martin-StPaul et al., 2017). More generally, exploring the mechanistic relevance of gap model parameters allows using functional trait databases to constrain them within realistic values and avoid equifinalities issues.

5.4 | Research avenues for a new generation of forest gap models

The large potential of forest dynamic models to tackle key questions in forest ecology has been reviewed elsewhere (Ruiz-Benito et al., 2020), but we highlight that their role in providing more robust predictions in response to global change components is increasingly emphasized (McDowell et al., 2020). Furthermore, we would like to focus on two related perspectives that are arising from the validation at both short and long term shown here.

5.4.1 | Biodiversity and ecosystem functioning in forests

The validation presented here opens perspectives for further tests of the effects of species richness or functional diversity on forest productivity. Several attempts were conducted to use gap models for studying diversity–productivity relationships (Bohn & Huth, 2017; Morin et al., 2011). Nevertheless, the models used had not been validated rigorously for monospecific forests across such a wide range of species and environmental conditions, although the analyses about the effect of diversity on ecosystem functioning strongly rely on the comparison with monospecific stands (Loreau & Hector, 2001, 2019). More precisely, the increased confidence in the ability of gap models to simulate monospecific stands will improve their ability to test non-additive effects in species mixtures (Gamfeldt & Roger, 2017), that is, effects directly related to interspecific interactions, together with their ability to return consistent results for mixed stands, as also checked in this study. Furthermore, as ForCEEPS accurately predicts stand productivity and long-term composition for the main species in Western Europe under a wide range of conditions, we may expect a high robustness of the simulated BEF relationship.

Forest gap models simulate local interactions among trees, which have been reported as fundamental drivers of mixture effects on forest functioning (Fichtner et al., 2018). Thus, the simulated biodiversity patterns necessarily emerge from selection and complementarity effects (Loreau & Hector, 2001), the latter referring to niche differentiation processes among co-existing species (as detailed in Morin et al., 2011) but also facilitative processes, depending on the model structure. Niche differentiation processes notably include complementarity in occupying canopy space (Jucker et al., 2015; Williams et al., 2017), and the 2D crown representation of ForCEEPS enables to better explore the way canopy packing occurs in simulated mixtures and affects forest productivity. More generally, a growing body of evidence suggests that structural diversity is a key driver of productivity in forests, independently of the potential effects of other facets of diversity such as species richness and functional diversity (Aponte et al., 2020; Dănescu et al., 2016; Gough et al., 2019; Schnabel et al., 2019). ForCEEPS is a suitable tool to quantify the importance of these—often tangled—diversity facets across large environmental gradients, with important consequence for our understating of BEF relationships and for the management of diverse forests.

Intraspecific variability in crowns (or more precisely tree foliage area) is simulated in ForCEEPS as a result of (a) neighbourhood-mediated plasticity induced by local shading conditions and (b) responses to environmental fluctuations (e.g. climate). Intraspecific crown plasticity was indeed shown to increase the efficiency of space use and the productivity in a number of mixed stands (Kunz et al., 2019; Williams et al., 2017). Furthermore, we acknowledge that intraspecific changes in crown architecture are ultimately determined by changes in within-tree biomass allocation and branching patterns, which have been shown to occur in mixed stands (Guillemot et al., 2020; Kunz et al., 2019; Pretzsch, 2014) but are not considered here. The modelling of such mixture effects on allometry is currently hindered by data scarcity, and would probably necessitate implementing the spatial distribution of the simulated trees in the horizontal space (Forrester et al., 2018). As a consequence, intraspecific variability in crowns is commonly overlooked in individual-based forest dynamic models (Maréchaux & Chave, 2017; Seidl et al., 2012), unless a teleonomic hypothesis is made, such as the perfect-plasticity approximation (Strigul et al., 2008). The evaluation of ForCEEPS for predicting canopy packing along diversity gradients will be addressed in forthcoming studies.

5.4.2 | Testing coexistence mechanisms in the short and long term

Species coexistence in forest gap models is based on two main mechanisms: first, trade-offs arising from the life-history strategies such as high rates of colonization often being tied to low shade tolerance, or a typically short lifespan of early successional, fast-growing trees; and second, the fact that cyclical succession is occurring on each individual patch so that species with different properties are able to dominate during different parts of the cycle (Bazzaz, 1979; Rees et al., 2001). Exploring the relative importance of these mechanisms for allowing species coexistence of simulated communities but also for creating and maintaining diversity effects on ecosystem functioning is a promising avenue for gap model applications (Cordonnier, Kunstler, et al., 2018; Falster et al., 2017), especially if such an exploration is to be carried out across a large range of conditions. This may ultimately lead to the formulation of new hypotheses, for instance about the impact of climate change on species coexistence and forest functioning.

Finally, we also see further potential applications of models like ForCEEPS in the design of forest policy. Large-scale forest restoration and reforestation programmes are key to prevent the most deleterious effects of climate change in the coming decade (Lewis et al., 2019). Global initiatives such as the Bonn challenge are planning restoration at an unprecedented scale (Verdone & Seidl, 2017). Yet, we currently lack science-based guidelines for the design of productive and resilient forest plantations in most environmental contexts. As mixed-species plantations are thought to be a crucial nature-based solution for climate mitigation and adaptation (Paquette et al., 2018), a generic and validated tool such as ForCEEPS

can be used to explore 'management versus climate scenario' interactions and promote climate-smart forestry at large scale. Thus, a new generation of forest gap models could foster the transfer of BEF knowledge into forestry practice.

Generating new hypotheses from model outcomes is one of the main reasons of using models in ecology in the first place, together with the support they may provide for better understanding the systems and processes at play, and their ability to yield predictions across spatial and temporal scales (Levins, 1966). As they did for more than 50 years, we believe that gap models in general, and the ForCEEPS model presented here in particular, maintain a key role for these purposes in forest ecology and management. More generally, because they seek for generality while aiming at relying on functional processes, such models are likely to be highly relevant to provide robust predictions of ecosystem composition, structure and functioning in a context of very uncertain future for forests (McDowell et al., 2020).

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AUTHORS' CONTRIBUTIONS

X.M. conceived the original idea; F.d.C. and X.M. implemented the model in the CAPSIS platform, benefited from the Forclim model by H.B.; J.G. and X.M. designed the general methodology, M.T. helped in formatting the data and N.M.-S. carried out the trait-based analysis; B.P., M.C., M.V., G.S., N.M.-S., E.C., J.-M.L. and J.-M.O. provided part of the data; J.G. and X.M. analysed the results and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The observed and simulated data that support the findings of the study are available in the following link: https://doi.org/10.6084/m9.figshare.12445589.v1). The calibration data from the French NFI including tree diameter and growth are available at https://inventaire-forestier.ign.fr/spip.php?rubrique159.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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